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# The revival of the extended phenotype

*After more than 30 years, Dawkins' Extended Phenotype hypothesis is enriching evolutionary biology and inspiring potential applications*

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When Richard Dawkins published his book on the Extended Phenotype (EP) in 1982 (*The Extended Phenotype: The Long Reach of the Gene*), it was received as an interesting but relatively minor addition to evolutionary theory primarily confined to a few poster child examples such as beaver dams and termite nests. The interest in the EP quickly subsided but has revived again in recent years, mainly as a result of next-generation sequencing and molecular techniques that allow the study of relationships between genomes and phenotypes among organisms at a much finer level. It has opened up a huge field of investigation to include concepts such as evolutionary feedback and niche construction theory into a so-called integrated theory of evolution. This renewed interest in the EP is not just an academic interest but could enable applications in agriculture and medicine. There is also an environmental dimension by studying the close relationship between species and how this provides resilience against environmental changes, notably global climate change.

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The EP as originally drafted by Dawkins embraces several related but at the same time distinct aspects of evolution, some confined to single species and others extending to complex ecosystems. In fact, the original definition specified three distinct categories, which are still largely adhered to today. The first is confined to single species, under the heading of architecture. This includes beaver dams and termite nests, where the phenotype is the fitness of the construction for survival and reproduction. There is no other organism involved, at least not directly, although of course numerous microbes may inhabit and benefit from some aspects of the construction.

The second form of EP involves two organisms where one manipulates the behaviour of the other; these are typically parasites or pathogens and their hosts. Here, the genes of one have a direct impact on the phenotype of the other either through physical interaction or alteration of gene expression in the host. Variation in relevant genes associated with host behavioural modification provides the raw material for natural selection.

The third category of EP as originally recognized by Dawkins is called action at a distance. Unlike the second type, it does not involve direct contact, but trickery to alter behaviour. The best-known examples involve brood parasitism such as the cuckoo that persuades other birds to raise its young on its behalf, with the obvious benefit of saving resources for survival and reproduction. The material for selection is variation among genes responsible for the mimicry, such as producing eggs that resemble the host bird's eggs. The EP then is the behaviour of the host in falling for the trick. As it involves modification in behaviour, this category is sometimes considered a special case of the second and is not the biggest field of study in the EP realm.

## Extending the extended phenotype hypothesis

Since then a fourth category has emerged, almost a combination of the first and second, where the EP comprises both the housing structure and microorganisms associated with the host. The most obvious example is plant soil, which comprises abiotic elements like minerals, organic material and diverse microbiota of fungi and bacteria. The plant can influence the soil's composition both by controlling particular biota and by altering organic composition such as the timing of shedding leaves and the compounds left in them. Here, the EP is the soil and its composition, which can favour one plant species at the expense of another.

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Given its potential application in agriculture and ecology, this fourth category has become a major focus of research and instrumental in reviving interest in the EP concept. Host/parasite relationships under the second EP category have also attracted a lot of research because of their fundamental importance in studying evolutionary feedback where genetic changes in cohabiting organisms have mutual effects on each other.

This category can also include other cases of evolutionary feedback whereby changes in one organism feed through to others and then back again, as was noted by Nathan Bailey, a specialist in adaptive evolution at St Andrews University in the UK. "Evolutionary

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feedback is likely to occur quite widely", he said. "A good example would be coevolution, for example linking plants and pollinators". In this case, natural selection favours plants that produce flowers adapted to the pollinators over factors such as shape, colour and nectar composition. In turn, the pollinator adapts to extract nectar as efficiently as possible from its chosen flowers.

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The same concept can also be applied to sexual selection within a species. "Evolutionary feedback is central to sexual selection, in which the evolutionary elaboration of one sex's sexual traits, such as a signal, might be influenced by the evolutionary elaboration of the other sex's preferences for those signals", Bailey explained. In these cases, the EP is the coupled system, whether this is the plant/pollinator combination or the relationship between male and female mating behaviour.

### The survival of coral reefs

One specific example of a closely coupled symbiotic system of great environmental interest is the coral reef, threatened by rising temperatures and ocean acidification through rising carbon dioxide concentrations. Reefs can be regarded as EPs of the corals themselves and the species of algae with which they cohabit and rely on for nutrient production. In return, corals provide shelter and some nutrients, such as ammonium, which they excrete as waste products. Coral reefs are highly important ecosystems as they provide a sanctuary to around one quarter of all marine species. Understanding their resilience against ocean acidification and warming is therefore critical for conservation biology.

Until recently, there was a limited understanding of the role of diversity among both corals and algae in conferring resistance against environmental change. But around 5 years ago, the field began to use molecular markers to distinguish species and strains of the symbiotic algae that associate with corals. "This really opened up a new frontier, since it meant both host and symbiont genotypic diversity could be manipulated to explore the role of intraspecific diversity in marine symbiosis ecology and evolution", commented John Parkinson, who conducts research in this field at Oregon State University in the USA. "It's only been a few years, and while most of the key questions we raised remain unanswered, more researchers are actively investigating them, and we're starting to get a better sense of how host and symbiont genotypic diversity might be important in different contexts. For example, scientists have incorporated genotypic variation into experiments in the sea anemone model for corals, finding that different symbiont strains recolonize bleached hosts at different rates under thermal stress. This could be important in predicting colony recovery dynamics after a bleaching event".

One key finding already is that coral reefs are fortunately more resilient against environmental change than had been thought. "On the theoretical side, we know that our predictions of coral reef persistence depend a great deal on whether adaptive capacity is included in the model", Parkinson explained. "Clearly evolution is mitigating reef damage on some level, but it is unclear whether the rate of adaptation can keep pace with the rate of climate change".

Indeed, the whole reef ecosystem is much larger than just corals and algae and includes many other organisms collectively referred to as holobionts with varying roles in adaptation. This blurs the definition of EP and symbiosis, as Parkinson conceded. "The operational definition of symbiosis that I use is any close, protracted relationship among two or more different organisms. This implies proximity both in space and time, but how much proximity? Corals and dinoflagellate endosymbionts are joined at the most fundamental level—the symbionts are located within the host cells so have proximity in space and they remain together for extended periods, so also have proximity in time. On the other hand, cleaner shrimp and the fish that they service sometimes only meet at specific cleaning stations and for only brief periods. Both are mutualistic symbioses, but they differ in their extent of integration".

### Host/parasite interactions

Indeed, any ecosystem has different levels of symbiosis, and it is hard to analyse the role genetic variation plays in more distantly connected species. The same holds for studying host/parasite relationships, which, so far, has been confined to relatively clear-cut cases involving just two organisms. There are some well-known examples of such relationships between a specific parasite and its host where the latter suffers badly and often ends up being destroyed to facilitate either the parasite's reproduction or escape into some other host to complete its lifecycle.

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One example is the case of orthopteran insects—grasshoppers or crickets—that are infected by the parasitic nematomorph hairworm. The worm's larvae develop inside the insect and induce it to jump into water to allow the grown parasite to exit and continue its lifecycle there [1]. The exact mechanism is still not clear, but it seems that the parasite alters expression of genes involved in the insect's visual and central nervous system making it seek out areas of water at night, which tend to be slightly illuminated compared with surrounding land [2].

In some cases, parasites induce structural changes in their host as the EP to boost their own reproductive or survival prospects. One well-studied case is the trematode or fluke *Ribeiroia ondatrae*, which causes severe deformity in amphibian hosts by interfering with limb development [3]. "Currently we are investigating how, precisely, these trematodes alter host development", commented Pieter Johnson from the University of Colorado. "For instance, is the mechanism mechanical, with cysts simply obstructing the host limb field, or do the parasites secrete a substance that mimics or alters the host's own hormones?"

Given that such questions are hard enough to answer in what appear like clear-cut cases of parasitic interference, the situation is much more complex when multiple parasites are involved. As Johnson noted, that has not been studied much largely because of the complexities involved.

 

"There have been some discussions of 'hitch-hiker' parasites but not much truly mechanistic work on competing forms of manipulation", he said.

A general problem when studying interactions between hosts and parasites lies in determining when alterations in behaviour are truly selective, as would seem in cases where suicide or severe deformity is caused. "The challenge often becomes identifying which of these are adaptive manipulations versus by-products of infection, for example pathology and morbidity", Johnson explained. "The latter is much harder to demonstrate compellingly. It often requires a deeper mechanistic look at how parasites are altering the host, for instance through genomic and transcriptomic approaches. It can also be difficult to demonstrate an increase in parasite transmission due to the altered phenotype under realistic, that is natural, conditions".

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Another question is whether alterations in behaviour occur in more than one host if parasites infect multiple hosts during their lifecycle. Johnson's experience is that changes in behaviour almost invariably occur in intermediate hosts to help the parasite with dispersal. Any changes in the ultimate host tend to be coincidental consequences of infection. A good example is malaria-causing *Plasmodium*, which induces female mosquitos to be attracted to human odour so that they are more likely to bite and infect the ultimate host [4]. Humans suffer from fever, but this is caused by the immune system rather than the parasite.

### Plants, soils and microbiota

Interactions between plants and soils are another major research area with both fundamental and practical interest. There is a general distinction between soils where one plant is dominant and the more common situation where many coexist or even compete in the same ecosystem. In the first case, there is clear evidence that the plant exerts some control over its environment, especially in the case of woods or forests where dominant tree species are able to prevent much growth underneath through lack of light. The deciduous cottonwood tree, a poplar, is one of the best studied in terms of recruiting soil as an EP: recent work has identified the soil microbial community and found strong associations between plant genotype, litter decomposition and soil community structure [5].

In this case, there is no evidence that the soil is manipulated to deter competitors, perhaps because the effect of the tree's shade is sufficient. But in the case of smaller plants, there is more of an incentive to influence the soil to deter competitors. There is evidence of this for *Allaria petiolate*, or garlic mustard. The plant produces allelochemicals, which are secondary metabolites of no direct value for the organism and toxic to mycorrhizal fungi in the soil. The result is to reduce the amount of the fungi upon which many other plants in the community rely [6]. However, the situation is again more complex and nuanced than these examples might suggest. In the case of garlic mustard, soil microbial communities tend to recover over time and gain some resistance, while the plant reduces its production of allelochemicals, which presumably incur some metabolic cost [6].

Casey Terhorst, an evolutionary ecologist at California State University, Northridge, USA, pointed out that, indeed, the impact of plants on their soils can be negative as well as positive. He suggested this might have wider benefits for the ecosystem as a whole, although how that works selectively is not clear. One clue may lie in the fact that relationships between plants and soils differ not just between genotypes and whole species, but also over time and by season. "There are lots of cases where plants condition the soil in such a way as to be less favourable to their own species", he said. "This can be important in preventing dominance by one species, as it causes the soil environment to constantly favour species that are not the dominant species. This can be an important factor in moving plants through successional phases". He is referring here to ecological succession, the process by which an ecosystem begins with a small number of pioneering plant and animal species, which gradually increases in number and diversity over time until it reaches a state of relative self-sustaining stability.

Terhorst added that the impact of plants on soils was much harder to detect when no single species is dominant, which has implications in agriculture. "Many farmers plant monocultures of a particular plant year after year", he explained. "The effects of plants on soils are probably more difficult to detect when farmers rotate crops annually, or when a diverse array of plants have strong influences on the soil, especially when different species influence the soil in different directions".

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The one common point is that the whole ecosystem is the extended phenotype, with plants and soils indirectly affecting each other through the microbiota. "While plants cannot impose selection on the soil directly because the soil does not reproduce, many of its abiotic properties are driven by microbes, bacteria and fungi, and those microbes in turn can impose selection on the plants. So you can get an eco-evolutionary feedback in which the plants impose selection on the microbes, which then evolve and change the ecological environment in the soil", Terhorst said. "That new ecological environment imposes selection on the plants, which can then evolve and have additional effects on the microbes in the soil again, which may be the same as before or different".

### Applications in agriculture and conservation

When combined with techniques to analyse the impact of field management on soils and microbiota, these insights on co-evolution and selection can inform agriculture. These are still early days, but studies have already demonstrated that, for instance, increasing the diversity of crop rotation feeds back into the soils and restores the associated ecosystems back closer to their historical state before monocultural crop production [7]. The finding that a greater diversity of crops would enrich the associated ecosystem and in turn boost nutrient production might seem obvious, but such studies provide the evidence. Another benefit of more diverse soils and crop rotation is that these techniques can sustain crop production all the year round in temperate regions such as Europe and the USA.

Similarly, research into the interactions between plants and soils is already finding applications in restoration and climate change mitigation. “For example, in restoration, practices need to take into account co-evolved communities of plants that are transplanted as an intact whole rather than a mix and match of the same species from different sites”, explained Thomas Whitham, whose work covers relationship between genes and ecosystems at Northern Arizona University, USA. “With climate change, what is locally adapted to the abiotic and biotic environment today will likely be maladapted to the future environment, so we need to include genetics into climate change modelling. [. . .] Simultaneously, we need to identify what non-local populations should be used in restoration to survive future conditions, what mutualists they should be inoculated with and what key genetics-based interactions are essential to maintain to support biodiversity”.

#### Enriching evolutionary theory

The EP concept has also been absorbed into the continuing debates about evolutionary theory, especially regarding the relationship between genes and the environment. The key point is the idea of extending evolution to include two-way feedback with the environment rather than just a process of adaptation into what is known as the extended evolutionary synthesis (EES). One of its advocates is John Odling-Smee, a proponent of niche construction theory at Oxford University, UK. He commented that Dawkins had underestimated the impact of his EP concept when he introduced it and that it had helped to lead the way towards ideas of extended evolutionary synthesis.

This is based on two unifying concepts: constructive development and reciprocal causation. The constructive development idea is itself controversial because it smacks of a return to Lamarckism that had previously been discarded, whereby organisms to some extent shape their own evolution by constantly responding to and causing changes in both their internal state and their external environment. The second concept, biological causation, flows from parents down to children through epigenetic adaptation and inheritance, and between organism and their environment. Indeed, epigenetic changes involving gene expression can be regarded as EPs, because they are mediated by the environment. These epigenetic changes can even be transmitted to the next generation, which seems to be an important evolutionary pathway to adaptation in organisms where genetic variation is lacking, such as small asexual populations [8]

Odling-Smee argues that, rather than being regarded as occasional outliers to Neo-Darwinism, epigenetic inheritance should be incorporated in a coherent integrated theory of evolution. He referred to the integrative Extended Evolution Synthesis project (http://extendedevolutionarysynthesis.com/) to extend evolutionary theory by bringing together the reciprocal interactions between long-term genetic evolution and short-term phenotypic plasticity. The aim is to establish the EES on a firm scientific basis and analyse how epigenetic plasticity can influence developmental regulation and in turn steer longer-term genetic change. The thinking here is that, given the obvious advantages of short-term plasticity to cope with environmental fluctuations that may or may not persist, genomes would evolve to incorporate the necessary epigenetic adaptability over time.

What is beyond doubt then is that the original EP concept is alive and well and has become a seed corn for research into evolution and coexistence within ecosystems of varying complexities. On the practical side, it is timely as a better understanding of the co-evolution of species in complex ecosystems has great potential for agricultural applications and for conservation and mitigating climate change.

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